

A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples

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ABSTRACT

A comprehensive comparison is provided for the first time for arthropod-assemblage compositions in Rovno and Baltic ambers, based on representative samples from Klesov (Pugach) and Dubrovitsa (Vol'noje) quarries (1256 fossils) and Yantarny quarry (757 fossils), respectively. A representative collection of Baltic amber was taken in Yantarny at the local mining factory (only smaller pieces that fitted through a 32 mm sieve were selected). A representative collection of Rovno amber was taken at the factory "UkrAmber" (Rovno). Results indicate the compositions of the assemblages to be different enough to consider the origin of Rovno and Baltic ambers as geographically different. The relative abundance of mites (Acari) in the Rovno sample is 0.6 times that in the Baltic sample (the share of dominant "*Acarus*" *rhombeus* Koch & Berendt in the Rovno sample is 0.3 times that in Baltic amber), and the relative abundance of Homoptera in the Rovno sample is almost half of that in the Baltic sample (mainly due to relative rarity of both the dominant aphid *Germaraphis*, whose share is 0.2 times that in the Baltic sample, and the scale insects). Within Diptera, the proportion of Chironomidae is almost half, and Sciaridae twice that of the Baltic sample. In terms of ants (Formicidae), the proportion of *Ctenobethylus goepperti* (Mayr) in the Rovno sample is half of that in the Baltic sample. The most striking are differences in species-level composition: 9 of 37 ants found in the Rovno representative sample belong to species and genera unknown in Baltic amber. Some differences encountered are of an ecological nature: aquatic and subaquatic arthropods are comparatively rare and leaf-litter dwellers of the *Sciara* zone are very abundant in Rovno amber. The age of the Baltic amber and stratigraphic correlation of the amber-bearing Prussian Formation are also considered in some detail. It is concluded that the proposal for their Ypresian–Lutetian age contradicts a wide array of the palaeontological, radiological, and stratigraphic data and thus cannot be accepted on the basis of available evidence.

KEY WORDS: Amber, Baltic, Rovno, Arthropoda, Insecta, faunal assemblage, inclusions, Eocene.

INTRODUCTION

The Late Eocene Baltic amber fauna has already been examined for more than 200 years. During this period, over 3000 species of animals and more than 100 species of plants have been described or indicated (Zherikhin 1978; Rasnitsyn & Quicke 2002). No other fossil locality is comparable with Baltic amber in terms of this diversity, and amber inclusions undoubtedly belong to those most widely known among lay people. Such a reputation does not, however, guarantee irrefutable knowledge of the Baltic amber fauna (Zherikhin & Eskov, in press). One of the problems yet to be resolved is the primary composition of the amber fauna. The available collections are biased because of overrepresentation of the most spectacular, rare, or otherwise more interesting inclusions, and this is at the expense of other 'trivial' fossils. This problem may be solved only by purposeful creation and study of representative collections whose original taxonomic composition of the fossil assemblage is minimally modified.

Previously, the only sample of the Baltic amber considered representative (that is, with minimally distorted original taxonomic composition of the fossil assemblage) was

the collection from Palmnicken (now Yantarny) described by Klebs (1910), further referred to as Klebs Coll. Recently, another representative collection which is kept at the Museum of Amber Inclusions at The University of Gdańsk has been described (Sontag 2003), further referred to as Sontag Coll. Unfortunately, its origin has been insufficiently specified ("3875 pieces of Baltic amber from Samland deposits (42.6 kg)" (Sontag 2003: 432).

The comparison of Klebs Coll. with Sontag Coll. and those described below indicates that the status of Klebs Coll., as a representative one, is not beyond doubt. Within Klebs Coll., the main problem is not even a low number of Acari (pointed out by Sontag who believes that this under-representation is a result of low-quality instruments used by Klebs). More serious is an unrealistically high abundance of Trichoptera compared to very low numbers of Hymenoptera (5.6% and 5.1% of all inclusions, respectively). The main problem is, however, different: Klebs used either the same source of amber as Sontag did, or one near-by. Being aware of the most productive varieties of the amber, Klebs nevertheless selected only 12 400 animal inclusions from 200 kg of amber with layered structure, while Sontag Coll. includes 42.6 kg of "unselected amber with layered structure" (Sontag 2003: 432), of which 1824 pieces weighing 22.3 kg, contained 7111 animal inclusions. In their material, the average weight of a piece of raw amber is similar (8.9 g in Klebs Coll. vs. 11 g in Sontag Coll.). At the same time, in Sontag Coll., an average inclusion-bearing piece of amber contains nearly three times more inclusions (3.9, or 0.32 inclusion per g) than in Klebs Coll. (1.6, or 0.17 per g). Given these discrepancies, it is not reasonable to consider Klebs Coll. as one that is truly representative.

Hoffeins and Hoffeins (2004) initiated a comparative study of the fauna of the Baltic and Bitterfeld (Saxonian) amber, driven by the inconsistency between Klebs's trichopteran data and their own results. They present statistics of inclusions in two big representative collections of the Baltic and Bitterfeld amber. The former collection originates from 11 different geographical sources taken together (further referred to as Hoffeins Baltic Coll.). The results found are unexpectedly similar for both collections, thus closing the discussion regarding the independent origin of Bitterfeld amber. The results obtained by Hoffeins and Hoffeins (2004) are in agreement with ours. This allows us an opportunity to use their data as representative collections of Baltic and Bitterfeld amber, within our analysis.

It should be mentioned that the proportion of Acari found in their collections is lower than in ours: the volume of gathered and examined collections is tremendous (574.3 kg), and thus it is possible that parts of small mites may have gone unnoticed. Our experience suggests that a more or less thorough selection of mites is possible only after multiple (more than ten times) examinations of one and the same sample. This, however, becomes an impossible task when faced with more than half a ton of amber.

Questions regarding the relationship between Baltic and Rovno amber, in addition to their areas of origin, have remained unresolved until recently. The reason for this is that there has been an absence of data on the fauna from Rovno amber.

To fill this gap, researchers from the Paleontological Institute, Russian Academy of Sciences (Moscow), and the Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine (Kiev), undertook special efforts to raise representative collections

TABLE 1

Representation of the main taxonomic groups of arthropods in the representative samples of Baltic (Brighton Coll., Sontag Coll., Hoffeins Baltic Coll.), Bitterfeld (Hoffeins & Hoffeins, 2004) and Rovno amber.*

Taxa	Brighton Coll.	Sontag Coll.	Hoffeins Baltic Coll.	Hoffeins Bitterfeld Coll.	Representative Rovno Coll.
Pseudoscorpiones	2	+	6 (0.1%)	21 (0.1%)	1
Opiliones	3 (0.4%)	+	10 (0.1%)	25 (0.2%)	4 (0.3%)
Aranei	24 (3.2%)	4.9%	359 (5.0%)	909 (6.1%)	40 (3.2%)
Acari	204 (27.0%)	24.0%	998 (13.9%)	2492 (16.8)	198 (16.0%)
Myriapoda	3 (0.4%)	+	17 (0.2%)	29 (0.2%)	2
Collembola	42 (5.6%)	8.0%	686 (9.6%)	1213 (8.2%)	86 (7.0%)
Archaeognatha	1	+	15 (0.2%)	16 (0.1%)	5 (0.4%)
Ephemeroptera	—	+	3	9	3
Odonata	—	—	1	1	—
Psocoptera	4 (0.5%)	+	37 (0.5%)	62 (0.4%)	5 (0.5%)
Thysanoptera	3 (0.4%)	0.7%	33 (0.5%)	44 (0.3%)	6 (0.5%)
Aphidoidea	31 (4.1%)	2.6%	—	—	24 (2.0%)
other Hemiptera	10 (1.3%)	1.9%	321 (4.5%)	673 (4.5%)	23 (1.9%)
Strepsiptera	—	—	2	—	—
Coleoptera	15 (2.0%)	3.0 %	312 (4.4%)	693 (4.7%)	64 (5.2%)
Neuroptera <i>s.l.</i>	—	+	4	6	—
Mecoptera	1	—	—	1	—
Trichoptera	2	0.8%	48 (0.7%)	81 (0.5%)	9 (0.7%)
Lepidoptera	7 (1.0%)	+	23 (0.3%)	70 (0.5%)	7 (0.6%)
Diptera	342 (45.3%)	42.7%	3676 (51.2%)	7128 (48.1%)	626 (50.7%)
Nematocera	279 (37.0%)	33.3%	2929 (40.8%)	5685 (38.4%)	518 (41.9%)
Brachycera	58 (7.7%)	5.8%	738 (10.3%)	1426 (9.6%)	104 (8.4%)
Formicidae	22 (2.9%)	3.7%	—	—	37 (3.0%)
other Hymenoptera	28 (3.7%)	2.9%	556 (7.7%)	1205 (8.1%)	50 (4.1%)
Blattoptera	2	+	31 (0.4%)	55 (0.4%)	5 (0.4%)
Isoptera	1	+	16 (0.2%)	33 (0.2%)	3
Mantodea	—	—	1	—	—
Plecoptera	—	+	4	2	—
Embioptera	1	—	—	—	1
Dermaptera	—	—	1	1	—
Orthoptera	1	—	8 (0.1%)	11 (0.1%)	—
TOTAL	755	6906	7177	14 808	1236

* Figures in the Total row differ from those given in various places in the text for the following reasons: 755 (not 757) in the Brighton Coll. column and 1236 (not 1256) in the Representative Rovno Coll. column differ because within the Arachnids, records which are based on the identification of particular spider webs, and not the actual specimens themselves, are not included; 7177 (not 7168) in the Hoffeins Baltic Coll. column, and 14 808 (not 14 780) in the Hoffeins Bitterfeld Coll. column differ because *incertae sedis* specimens are considered (although not shown separately in the table); the same for the Brighton Coll. (755, not 749) and the Representative Rovno Coll. (1236, not 1199).

of both Baltic and Rovno amber inclusions. A representative collection of Baltic amber has been extracted in Yantarny at the local mining factory (only pieces smaller than 32 mm were selected). Another representative collection, as well as the majority of other amber inclusions from the collection of the Schmalhausen Institute of Zoology, has been extracted in Rovno at the State Enterprise “UkrAmber” (only pieces of 2–50 g were selected). The present article is based on these two collections and includes published information concerning other representative collections. The purpose is to shed light on relationships between the respective entomofaunas.

TABLE 2

Composition of the arthropod fossils in Baltic amber (Brighton Coll.) and Rovno amber (Representative Rovno Coll.). Names of orders and higher level taxa are in bold; suborders are bold italic; genus and species names are italic and subfamilies of ants are given in brackets. Fossils not identified with confidence are considered in totals even if not shown in the table. The percentage of a particular order reflects the proportion of that order among all arthropods, and figures in brackets refer to the proportion of an insect order among Insecta *s.str.* Percentages of families and genera refer to proportions of those particular taxa within the corresponding order. Percentages may not be given for taxa represented by only one or two specimens in a particular sample. Figures are approximate.

Taxa	Brighton Coll.		Representative Rovno Coll.	
	n	%	n	%
Pseudoscorpiones	2	0.3	1	
Dithidae: <i>Heterolophus</i> sp.	1		—	
Opiliones	3	0.4	4	0.3
Aranei	24	3.2	40	3.2
Amaurobiidae	1		—	
Araneidae	1		2	
Dysderoidea	1		—	
Nesticidae: <i>Acrometa cristata</i> Petrunkevitch	—		1	
Eusparassidae	1		—	
Oonopidae	2	8.3	5	12.8
Salticidae	2		2	
Linyphiidae	—		1	
Liocranidae	—		1	
Zodariidae:				
<i>Adorator ?hispidus</i> (Koch et Berendt)	—		1	
Theridiidae	5	21	13	33.3
Spider web	2	0.3	20	1.6
Acari	204	27.0	198	15.8
Digamasellidae	—		2	
Phytoseiidae	1		—	
?Ixodidae	—		2	
Gamasina indet.	—		1	
Parasitiformes indet.	1		—	
Glycyphagidae:				
<i>"Acarus" rhombeus</i> Koch et Berendt	116	56.9 (15.3 of all arthropods)	62	31.3 (4.9 of all arthropods)
Astigmata (Acaridia) indet.	—		7	3.5
Oribatei: cf. <i>Licneremaeus fritschi</i> Sellnick	1		—	
Damaeidae	1		—	
Oppoidea	—		1	
?Cepheidae	—		1	
Liacaroidea	—		1	
Brachypilina indet.	—		1	
Oribatida indet.	18	8.8	14	7.0
Bdellidae	—		1	
?Rhagidiidae	—		1	
Anystidae	—		9	4.6
Cheyletoidea	—		2	
Erythraeidae	—		4	2.0
Microtrombidiidae	—		5	2.5
Parasitengona indet.	—		9	4.6
Trombidiiformes indet.	54	26.5	4	2.0
Acari indet.	12		71	
Diplopoda	3	0.4	1	
Polyxenidae: <i>Polyxenus</i> sp.	2		1	
Chilopoda : Lithobiidae: <i>Lithobius</i> sp.	—		1	
Collembola	42	5.6	86	6.9
Entomobryidae	16	38.1	46	54
Tomoceridae	—		1	
Entomobryomorpha indet.	6		5	
Hypogastruridae	—		3	3.5

Taxa	Brighton Coll.		Representative Rovno Coll.	
	n	%	n	%
Sminthuridae	9	21.4	13	15.1
Bourletiellidae	—		2	
Symphyleona indet.	—		2	
Archaeognatha	1		5	0.3 (0.4)
Machilidae: <i>Machilis</i> sp.	—		5	
Ephemeroptera	—		3	
Psocoptera	4	0.5 (0.8)	5	0.4 (0.6)
Caeciliusidae	1		1	
Psocidae	2		1	
Sphaeropsocidae:				
<i>Sphaeropsocus kuenowii</i> Hagen	1		—	
Thysanoptera	3	0.4 (0.6)	6	0.5 (0.6)
Homoptera	41	5.4 (8.6)	43	3.4 (4.8)
Sternorrhyncha	39	5.2 (8.2)	32	2.6 (3.5)
Elektraphididae: <i>Schizoneurites</i> sp.	2		—	
Mindaridae: <i>Mindarus</i> sp.	1		1	
Eriosomatidae: <i>Germaraphis</i> sp.	27	65.9 (5.7 of all insects)	10	23.4 (1.1 of all insects)
Drepanosiphidae	—		10	23.4
Aphidomorpha indet.	1		3	
Matsucoccidae: <i>Matsucoccus</i> sp.	2		2	
Ortheziidae	—		1	
Coccoomorpha indet.	6		3	
Aleyrodidae	—		2	
Auchenorrhyncha	2		11	0.9 (1.2)
Cicadellidae	2		3	7.1
Heteroptera	—		4	0.3 (0.4)
Microphysidae:				
<i>Loricula perkovskyi</i> Putshkov & Popov	—		1	
Miridae	—		1	
Anthocoridae	—		1	
Coleoptera	15	2.0 (3.2)	64	5.1 (7.1)
Carabidae: <i>Dromius</i> sp.	1		—	
Staphylinidae	2	13.3	9	13.9
Pselaphinae	1		7	
Scydmaenidae	2	13.3	5	7.7
Ptiliidae	—		3	4.9
Melyridae	1	6.7	1	1.6
Helodidae	—		4	6.2
Anobiidae	3	20.0	1	1.6
Dryophilinae	2		—	
Cleridae	—		1	
Elateridae	—		7	10.8
Artematopidae	—		1	
Lathridiidae	1		1	
Zopheridae	—		1	
Languriidae	—		1	
Melandryidae	—		2	
Scraptiidae	1	6.7	2	3.1
Aderidae	1	6.7	5	7.6
Anthicidae	—		1	
Mordellidae	1	6.7	4	6.1
Curculionidae: Scolytinae	—		4	6.1
Polyphaga indet.	1		6	
Mecoptera	1		—	
Bittacidae: <i>Hylobittacus fossilis</i> (Carpenter)	1		—	
Trichoptera	2		9	0.7 (1.0)
Ecnomidae: <i>Archaeotinaodes</i> ? sp.	1		—	
Philopotamidae	—		1	
Polycentropodidae	—		3	33
Hydroptilidae	—		1	
Phryganeidae?	—		1	

TABLE 2 (continued)

Taxa	Brighton Coll.		Representative Rovno Coll.	
	n	%	n	%
Lepidoptera	7	0.9 (1.5)	7	0.6 (0.8)
Gelechioidea	—		1	
Diptera	342	45 (71.7)	626	50.0 (69.2)
Nematocera	279	37 (59)	518	41 (58)
Tipulidae	—		4	0.6
Limoniidae	3	0.9	38	6.1
Tipuloidea indet.	2		9	
Ptychopteridae?	1		—	
Psychodidae	6	1.8	16	2.6
Chironomidae	139	40.6	137	21.9
Ceratopogonidae	20	5.9	29	4.6
Chironomoidea indet.	3	1.2	1	
Simuliidae	1		—	
Mycetophilidae	13	3.8	18	2.9
Keroplastidae	9	2.6	27	4.3
Mycetophilidae or Keroplastidae	2		10	
Mycetobiidae	—		1	
Sciaridae	52	15.2	189	30.1
Cecidomyiidae	24	7.0	23	3.7
Scatopsidae	—		3	0.5
Nematocera indet.	5		13	
Brachycera	58	7.7 (12)	104	8.3 (12)
Empididae	12	3.5	7	1.1
Dolichopodidae	38	11.1	64	10.2
Empidoidea indet.	1		—	
Bombyliidae?	—		1	
Rhagionidae	—		4	0.6
Syrphidae: Syrphinae	2		—	
Phoridae	3	0.9	18	2.9
Anthomyiidae?	1		—	
Diptera Schizophora indet.	1		—	
Brachycera indet.	—		10	
Hymenoptera	50	6.6 (10.5)	87	6.9 (9.6)
Megaspilidae	4	8	2	2.3
Ceraphronidae	—		1	
Bethylidae	—		1	
Proctotrupidae	1		—	
Diapriidae	6	12	8	9.2
Platygastridae	1	2	3	3.5
Scelionidae	3	6	16	18.4
Mymaromatidae	1	2	3	3.5
Mymaridae	3	6	5	5.8
Torymidae: <i>Monodontomerus</i> sp.	2		—	
Trichogrammatidae	—		2	
Aphelinidae	—		1	
Chalcidoidea indet.	1		—	
Ichneumonidae	3	6	—	
Braconidae	1	2	4	4.6
Ichneumonoidea indet.	1		—	
Formicidae	22	44 (4.6 of all insects)	37	43 (4.1 of all insects)
Blattoptera	2	0.3 (0.4)	5	0.4 (0.5)
Isoptera: Rhinotermitidae:				
<i>Reticulotermes antiquus</i> Heer	1		3	0.2 (0.3)
Embioptera	1		1	
Orthoptera Ensifera indet.	1		—	
TOTAL	757		1256	

MATERIAL

Baltic amber

Deposits bearing Baltic amber are abundant along the shores of the Baltic Sea from Lithuania to Jutland. In many places the amber was re-deposited, sometimes several times, as a result of erosion and glacial re-working of the amberiferous deposits.

The largest deposits are situated in Yantarny, Kaliningrad Region, and have been industrially mined since the end of the 19th century. The age of the richest amber-bearing deposits (so-called Blue Earth, or “Blau Erde” of German authors) is dated micro-faunistically as Late Eocene (Kaplan *et al.* 1977).

These results have been questioned by Ritzkowski (1997), who inferred a Middle Eocene age of the Prussian Formation based on radiometrically dated glauconite from the lower layer of the Blue Earth (44.1 ± 1 Ma) and the underlying Wild Earth (47.0 ± 1.5 Ma). However, these figures are based on two samples, each from the respective layers. We consider these data to be insufficient to disprove the results by Kaplan *et al.* (1977) for the absolute glauconite age of the Prussian Formation (37.7 ± 3 Ma), which was based on six samples. Furthermore, Grigelis *et al.* (1971) considers the glauconite of the Blue Earth and overlaying members of the Prussian Formation to be re-deposited. Further information is required to draw a final conclusion.

Further evidence stems from the presence of the zonal species *Globigerina corpulenta* (Subb.) in addition to a recent find of three species of planktonic foraminifers, viz. *Turborotalia centralis* (Cushman & Bermudez), *Truncorotaloides cf. rohri* Brönn. & Bermudez, *Globigerina praebulloides* Blow., in the Prussian Formation of “Primorsky” quarry in Yantarny (Kharin & Lukashina 2002). These foraminifers are common in the Upper Eocene of the Lublin Province in Poland. These findings imply correlation of the Prussian Formation with the foraminiferal zones P15–P17 of the Upper Eocene (Kharin & Lukashina 2002). The presence of a dinoflagellate *Charlesdowniea clathrata* (Eis.) Lentin & Vozzhen. does not contradict the above data, because in the dinoflagellate zonation the respective zone is referred to the Priabonian Stage of the Upper Eocene (Krasheninnikov & Akhmetiev 1996: 26).

A rich foraminiferan assemblage of the Prussian Formation from Rudamina borehole (Lithuania) is characteristic strictly of the Upper Eocene (Grigelis *et al.* 1971). The sponge spicules of the Prussian Formation resemble those in the Upper Eocene of Dnieper-Donets Palaeogene Basin (Ivanik 2003: 66). Well-studied palynological assemblages of the Prussian Formation “are typical of the Upper Eocene of Western Europe, European part and other areas of CIS” (Krasheninnikov & Akhmetiev 1996: 26).

The Prussian Formation transgressively overlaps the Alkas Formation and lower Palaeogene formations and in the west of the Sambian Peninsula, it is overlaid by the Lower Oligocene Palve Formation. The assemblage of planktonic foraminifers of the Alkas Formation suggests its Bartonian age (Middle Eocene) (Kaplan *et al.* 1977). The glauconite absolute date of the Alkas Formation is 41 ± 3.5 Ma (Bartonian/Lutetian boundary), and that of the Palve Formation is 34.6 ± 3 Ma (Kaplan *et al.* 1977) (near the Eocene/Oligocene boundary according to Berggren *et al.* 1995). Taking into account the overlapping ranges of the foraminiferal P12–P14 and nannoplankton NP15–NP16 zones, Grigelis *et al.* (1988: 46) came to a conclusion regarding the identical stratigraphical position of the Baltic Alkas Formation and West Belorussian Kiev Formation

which “belong to the upper half of the Lutetian and to the Bartonian stages, and correspond to the Bodrakian Regio-Stage of Crimea”. Thus, Ritzkowski’s proposal (1997) of the Ypresian–Lutetian age of the Prussian Formation (Lower–lower Middle Eocene), and, consequently, the Bartonian age of the Palve Formation (upper Middle Eocene), if accepted, would result in reconsideration of the entire stratigraphy of the Middle Eocene–Lower Oligocene of Eastern Europe.

Ritzkowski (1997: 22) points out that the disparity in dates of amber-bearing deposits (those at Chłapowo in Pomorze, former Pomerania, correspond to the Eocene/Oligocene boundary) suggests that the Baltic amber fauna existed, without any essential changes, for more than 20 Ma (“all Eocene and the beginning of Oligocene”). This seems unlikely since, firstly, it is well known that none of the amber-bearing deposits can be considered as their primary burial, and this includes Chłapowo. Secondly and more importantly, the Middle and Late Eocene was a time of rapid change in the insect fauna, as reflected by a series of Lagerstätten ranging from the Middle Eocene Lutetian (Green River in the USA, Messel, Eckfeld and Geiseltal in Germany) through to near the Eocene/Oligocene boundary (Florissant in the USA, Bolshaya Svetlovodnaya in Primorskiy Krai and Bembridge Marls in England). The Baltic assemblage occupies an intermediate position between these two groups of faunas (Rasnitsyn & Quicke 2002; Dlussky & Rasnitsyn 2003). Thus, the hypothesis regarding long stasis of the entomofauna during the second half of the Eocene appears implausible. We plan to devote a special paper to the age of Baltic amber in the near future.

In the Yantarny quarries the amber is mined by washing away the “Blue Earth”. The amber-bearing slurry is then piped into the industrial complex and successively sieved. In September 1992 and in June 1993 the team from the Arthropoda Laboratory, Paleontological Institute, Moscow, selected amber directly at the factory in Yantarny. A sample of raw amber was examined under the microscope, and the taxonomic position of all inclusions found was determined whenever possible, up to the order and family level. This level of identification is usually adequate in assessing the general composition of the fossil fauna. During two visits, 1382 (625+757) inclusions were found and identified. The collection of 1992 is included in a separate publication dealing mainly with the distribution of inclusions according to size fractions of the amber (Zherikhin & Eskov, in press). The composition of inclusions in the collection of 1993, as displayed at the order level in Table 1, and in more detail in Tables 2 & 3, is considered in this paper.

Rovno amber

Rovno amber with arthropod inclusions has been collected at the Klesov (the majority of inclusions), Dubrovitsa (less than one third of inclusions) and Vladimirets deposits (insignificant quantity) (all in the Rovno Region), which constitute a part of a vast area of the development of the amber-bearing layers in the north of the Rovno and Zhitomir regions, within the boundaries of Ukrainian Polesye (Perkovsky *et al.* 2003a). The industrial mining of amber in the Rovno Region began only recently. Before that, amber was taken in a primitive way from sandy-clay sediments of granite quarries in the outskirts of Klesov, from drainage-channel lumps, and from natural outcrops of amber-bearing deposits along river banks.

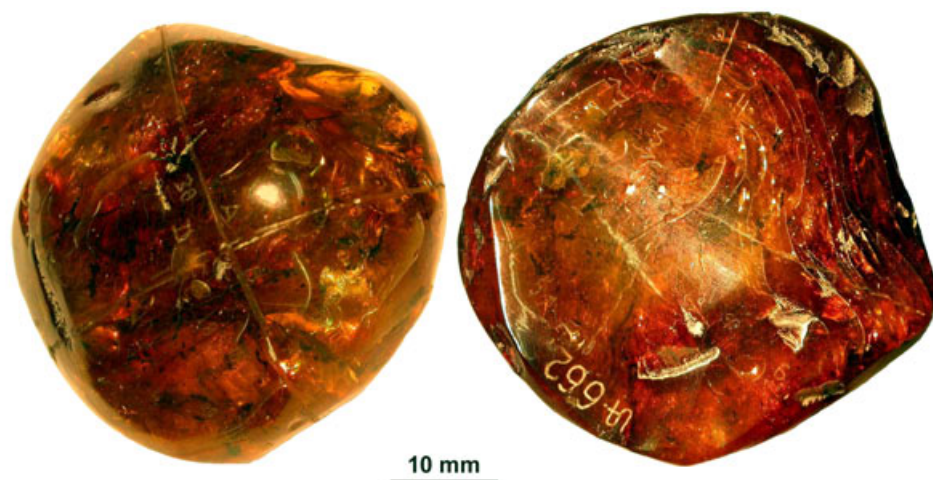


Fig. 1. A piece of Rovno amber (UA-662) with more than 50 inclusions.

The area where amber-bearing deposits developed is situated at the periphery of the north-western part of the Ukrainian Crystalline Rock Massif. Detailed information regarding the nature of Rovno amber deposits has already been published (Perkovsky *et al.* 2003a).

The Late Eocene age of the Obukhov Formation and the Early Oligocene age of the Mezhygorje Formation have been determined palaeontologically. According to A.B. Stotland (pers. comm.), dinocysts of the Obukhov Formation include index species of Zone *Charlesdowniea clathrata angulosa*–*Deflandria phosphoritica* and represent the zonal complex characteristic of the Obukhovian Regio-Stage in the stratotypical section, the Albian Regio-Stage of the Black Sea depression and Crimea, the Beloglinian Regio-Stage of the North Caucasus and the Priabonian Stage of Western Europe. The complex of palynomorphs with *Myrica pseudogranulata*–*Quercus gracilis*–*Q. graciliformis* is also characteristic of Upper Eocene deposits of various regions in the south of the East European Platform. The dinocyst complex of the Mezhygorje Formation (Perkovsky *et al.* 2003b) contains species characteristic of the Early Oligocene zonal assemblages, *Phthanoperidinium amoenum*–*Wetzeliella symmetrica*–*W. gochtii*. This corresponds with the dinoflora characteristic of the Mezhygorian Regio-Stage of the stratotype, the Borysthen Formation of the Black Sea depression, the *Planorbella* Beds of the Crimea, the Pshekhian Regio-Stage of the Northern Caucasus, and the Rupelian Stage of Western Europe.

As for the origin of amber from Ukrainian Polesye (Rovno amber), a hypothesis regarding its large-scale transport from elsewhere has been considered for some time. During the Late Eocene and Early Oligocene, the territory between north-western Europe and the southern Urals (the so-called Subparatethys Sedimentation Province) is known to have been covered by marine basins. However, the analysis of palaeogeographic and palaeosedimentary conditions during that time interval in the north-western part of the Ukrainian Crystalline Rock Massif, permits consideration of the amber from Ukrainian Polesye as autochthonous. An indirect confirmation of this is the Eocene age of the autochthonous amber from the Lublin province in Poland (Kasinski & Tolkowicz

1999), inferred from the amber-bearing deposits in Parchev, belonging to nannoplankton zones NP17–18 (Kosmowska-Ceranowicz *et al.* 1990).

Since both Baltic and Rovno ambers are succinite, a key to the problem of the origin of Rovno amber appears to be in analysis of their inclusions, as was predicted earlier (Zherikhin & Eskov 1999). For a long time, Rovno amber has been considered very poor in inclusions, even in comparison with Belorussian amber (Zherikhin & Eskov 1999). This was one of the main arguments against Rovno amber being autochthonous (Kosmowska-Ceranowicz *et al.* 1990). In fact, inclusions were simply destroyed or could not be used for research until the beginning of their purposeful selection at the “UkrAmber” factory (Rovno) by A. Vlaskin and E. Perkovsky for the Schmalhausen Institute of Zoology. For instance, one of the selected amber pieces weighing 30 gr (no. UA-662) was found to contain over 50 inclusions (Fig. 1).

Identification of the first hundred arthropods from the Rovno amber at the Arthropoda Laboratory indicated the peculiarity of its fauna. This was evident in the share of particular higher taxa in the assemblage, and by its species- and, sometimes, genus-level composition. Subsequent research has confirmed these preliminary results (Kasparyan 2001; Semenov *et al.* 2001; Simutnik 2001, 2002; Dlussky 2002; Dlussky & Perkovsky 2002; Kononova 2003; Perkovsky *et al.* 2003b; Putshkov & Popov 2003; Fedotova & Perkovsky 2004, 2005; Perkovsky & Fedotova 2004; Polilov & Perkovsky 2004; Popov 2004; Engel & Perkovsky 2006). By 2004, over 2300 pieces of Rovno amber with inclusions have been examined by the authors. The majority of pieces (2200) constitute the collection of the Schmalhausen Institute of Zoology, displaying 107 families of 19 insect orders (further referred to as Total Kiev Coll.).

Methodical selection of inclusions in Rovno amber began in 2000 at the factory “UkrAmber”. After having been mined, Rovno amber, like Baltic, is sorted into size fractions (depending on the weight of specimens). The amber with layered structure is sorted separately, based mainly on its lamination and visible internal pollution, irrespective of the weight of pieces. It is worth pointing out that unlike Baltic amber, the Rovno amber is covered by a 2 mm thick oxidised crust, which often makes identification of the type of amber difficult. In our and Weitschat’s (pers. comm., 2002) opinions, the thick oxidised crust of the Rovno amber, especially from Klesov, does not agree with the hypothesis regarding its long transportation, which would have resulted in considerable abrasion of the amber surface.

All inclusions in the collection were selected from translucent amber weighing 2–50 g, sourced from 120 kg of amber with a layered structure (with turbid, strongly polluted and foamy amber being excluded). These pieces were not sorted for or against any kinds of inclusion. All selected inclusions of total weight 12.3 kg were bought by the Schmalhausen Institute of Zoology in 2001–2002.

In total, the representative collection comprises 1256 remains of Arthropoda (993 insects *s.l.*, i.e. including Enthognatha) further referred to as the Representative Rovno Coll. The composition of orders, in comparison with other representative collections, is shown in Table 1. Besides succinite, a light-yellow easily melted piece of fossil resin weighing 30 g was found within layered Rovno amber, bearing seven inclusions of Chironomidae (Perkovsky & Vlaskin 2004). Together with this find, the total number of inclusions of Arthropoda recorded in 12.3 kg of amber with layered structure is 1263 (not including Diptera eggs). Table 2 shows a detailed composition of inclusions in

comparison with the Baltic representative collection of 1993. The latter collection contains 757 inclusions (519 insects *s.l.*) and is currently housed at the Booth Museum of Natural History (Brighton, England) further referred to as the Brighton Coll.

DISCUSSION

The correlation of taxonomic groups of Arthropoda in different samples of Baltic amber

Noticeable differences in inclusion composition in various collections of Baltic amber are widely known. This is usually accounted for by a biased representation (premeditated or unpremeditated preferential selection of one type of fossils and/or rejection of the others; Sontag 2003; Zherikhin & Eskov, in press). Sontag (2003), quoting relevant data on the biggest European collections—Zoological Museum in Copenhagen (Larsson 1978), Museum of the Earth in Warsaw (Kulicka 1990), Klebs Coll. (Klebs 1910) and Sontag Coll.—presented a possible explanation for these differences. In her opinion (Sontag 2003: 434), the main reason for differences in data among the authors mentioned, including her own, is, in the first two cases, the “influence of collector selection, resulting in low numbers of small arthropods such as Acari or Collembola, but in higher numbers of large Hymenoptera or Coleoptera”; and in the third case, the imperfection of optics used at the beginning of the 20th century. These are precisely the facts that explain, for instance, an abnormally low rate of small Acari in Klebs Coll. Although this explanation appears to be logical, it is not necessarily an exhaustive one.

To explain these differences, one should consider at least three groups of factors. These include the influence of the quality of the instruments used, mentioned by Sontag (2003) (in our opinion, expertise of collectors and their working conditions in general); heterogeneity of the raw amber material, pointed out by Zherikhin (fossils from different parts of run-off area can be buried together); and the different fossil assemblages in pieces of different size (Zherikhin & Eskov, in press). Additional sources of uncertainty could include the highly seasonal occurrence of some groups like Chironomidae and aggregations of some other groups, e.g. the mite “*Acarus*” *rhombeus* Koch & Berendt and the pennicillate millipede *Polyxenus* Goldfuss.

The importance of differences in origin of various samples of Baltic amber is also beyond doubt. But there is insufficient data available to substantiate this hypothesis. In order to gain some perspective on the origin of Baltic samples, it would be beneficial to compare the composition of assemblages from Yantarny and the northern coast of the Jutland. Unfortunately, the Danish representative collection is not yet available for study. However, a comparative analysis of the ant composition in Danish and other Baltic samples, is currently in progress (G.M. Dlussky pers. comm., 2005). An analysis of the influence of the size of amber pieces will have to be postponed until Zherikhin and Eskov’s article is published.

Comparative study of Baltic and Rovno amber

The problems discussed above favour cautious consideration in dealing with relationships between Baltic and Rovno amber. This includes questions as to whether or not these two amber types had the same origin; whether they came from different parts of the same river basin, or whether they originated from entirely different basins within the same continental mass.

TABLE 3

Composition of ants (Formicidae) in representative samples of Baltic amber (Brighton Coll.) and Rovno amber (Representative Rovno Coll.); subfamilies of ants and respective figures are given in bold. Fossils not identified with confidence are considered in totals even if not shown in the table.

Taxa	Brighton Coll.		Representative Rovno Coll.	
	n	%	n	%
Dolichoderinae	14	63.6	16	43.2
<i>Ctenobethylus goepperti</i> (Mayr)	13	59.1	11	29.7
<i>Iridomyrmex geinitzi</i> Mayr	—		1	
<i>Dolichoderus polesus</i> Dlussky	—		1	
<i>Dolichoderus</i> sp. n.	—		1	
Formicinae	8	36.4	11	29.7
<i>Camponotus menzei</i> Mayr	1		—	
<i>Formica flori</i> Mayr	1		1	
<i>Lasius schiefferdeckeri</i> Mayr	4	18.2	6	16.2
<i>Plagiolepis minutissima</i> Dlussky	—		2	
<i>Prenolepis henschei</i> Mayr	1		—	
Myrmicinae	—		6	16.2
<i>Aphaenogaster antiqua</i> Dlussky	—		1	
<i>Oligomyrmex nitidus</i> Dlussky	—		1	
<i>Oligomyrmex ucrainicus</i> Dlussky	—		1	
<i>Leptothorax</i> sp.	—		1	
Myrmicinae gen. et sp. n.	—		2	
Ponerinae	—		1	2.7
<i>Gnamptogenys europaea</i> (Mayr)	—		1	
Pseudomyrmecinae	—		1	2.7
<i>Tetraponera simplex</i> (Mayr)	—		1	
Formicidae indet.	—		2	5.4
TOTAL	22	100	37	100

The general faunal composition of Rovno amber at the level of taxa of the highest rank (Table 1) gives definite, but not necessarily reliable, evidence, making it distinct from Baltic amber. This is supported by the essentially lower number of Aphidinea and Acari, in comparison with any of the representative samples of Baltic amber which has been analysed. The reliable, distinguishing features of the Rovno and Baltic amber faunas at the species level (e.g. Formicidae) allow us to make preliminary conclusions as to the differences in faunal origins of Rovno and Baltic amber, i.e. it is most likely that they were formed in different areas of Late Eocene Europe.

Dlussky and Perkovsky (2002) showed that Rovno amber contains an extremely high number of new species (26% of all identifiable specimens). New Baltic amber collections of the same volume have only 2–5% of new species. In Rovno amber, Dlussky described five new species of Dolichoderinae (Dlussky 2002; Dlussky & Perkovsky 2002), one species of Formicinae and three species of Myrmicinae (Dlussky & Perkovsky 2002). Four new species and one new genus are yet to be described (Dlussky, pers. comm.).

Worth mentioning is the difference in representation of the main Formicidae subfamilies (Table 3). The figures given by Dlussky and Perkovsky (2002) for the ants from Representative Rovno Coll. need to be corrected, because six specimens do not belong to Representative Rovno Coll. and were included in the calculations by mistake. The corrected figures are as follows: Representative Rovno Coll. contains noticeably fewer Dolichoderinae (43% vs. 64% in Brighton Coll.), and the number of Myrmicinae

is, on the contrary, increased (16% vs. nil). At least 9 of 37 specimens belong to new species and genera unknown in Baltic amber.

Similarly, upon examination of 41 Rovno amber spiders, Wunderlich (2004) described or indicated a number of taxa never recorded in the amber of Samland origin, viz. *Balticonopsis perkovskyi* Wunderlich, *Fossilanapis* sp. indet., Anapidae indet., *Succinero rovnoensis* Wunderlich and *Gorgopsina fractura* Wunderlich. The families Anapidae, Mimetidae and Salticidae are, however, well studied in Samlandic amber. A quarter of the adult male spiders (Aranei) from Rovno amber belong to new species. All gall-midges from the Representative Rovno Coll., which have been identified to the species level (including *Campylomyza superposita* Fedotova and *Didimomyia accidentalis* Fedotova (Fedotova & Perkovsky 2004, 2005)) are found to be unknown in the Baltic amber.

The comparison of arthropod composition, identified in the more thoroughly studied collections (Representative Rovno Coll. and Brighton Coll.; Table 2), reveals additional, and in some cases significant, differences. The Representative Rovno Coll. contains almost half as many Homoptera (4.8% vs. 8.6%) (6.8% of insects *s.str.* in Sontag Coll.) and rather many Collembola (6.9% vs. 5.6%; 7.8% in Sontag Coll.). The abundance of Collembola, in particular, does not allow us to explain the small number of Acari by assuming that Rovno amber is poor in small arthropod inclusions. Under-representation of mites (Acari) in the Representative Rovno Coll. (15.8% vs. 27.0%; 24% in Sontag Coll.) is due to the relative scarcity of “*Acarus*” *rhombeus*: 31.3% in Representative Rovno Coll. vs. 56.9% of all mites in the Brighton Coll. The majority (65%) of *A. rhombeus* in the Representative Rovno Coll. have been found in two pieces of amber, one containing *Machilis*, and the other containing cockroaches. The origin of these amber pieces may have been associated with a relatively wetter habitat. In the Brighton Coll., two pieces, which are richest in this species, produce only 33.6% of all *A. rhombeus* in the sample. The rest of the mites together constitute 10.8% of all arthropods (11.3% of all arthropods identified to the order level) in the Representative Rovno Coll., and 11.6% (11.8% of all arthropods identified to the order level) in the Brighton Coll.

Among the Collembola of the Representative Rovno Coll., the Entomobryidae are more dominant than in the Brighton Coll. (Table 2). Out of 139 Collembola of the Total Kiev Coll. identified to families, 59.7% are Entomobryidae and 24.5% are Sminthuridae. The collembolan assemblage would seem to indicate that the climate of the Rovno amber forest was relatively dry.

The decreasing number of Homoptera in Rovno amber results primarily from the low representation of *Germaraphis* aphids: this genus accounts for 65.9% of Homoptera (5.7% of all insects) in the Brighton Coll. versus 23.4% (1.1% of all insects) in the Representative Rovno Coll. (Table 2). Rovno amber (Representative Rovno Coll.) contains noticeably fewer scale insects: their proportion among all insects (0.66%) is 2.6 times that in the Brighton Coll. (1.68%; 1.69% in Sontag Coll.). Only two small larvae of *Germaraphis* constitute a part of a syninclusion in the Representative Rovno Coll., while in the Brighton Coll., the syninclusions, containing more than one specimen of *Germaraphis*, account for 55.6% of all *Germaraphis*. The proportion of Auchenorrhyncha among Homoptera in the Representative Rovno Coll. is much higher – 26.1% vs. 4.9% (10.1% in Sontag Coll.).

The dipteran proportion in the Representative Rovno Coll. is similar to that in the Brighton Coll. – 69.3% vs. 71.7% (67.3% in Sontag Coll., 72.1% in Hoffeins Baltic

TABLE 4

Composition of Diptera in the representative samples of Baltic (Brighton Coll., Sontag Coll., Hoffeins Baltic Coll.), Bitterfeld (Hoffeins Bitterfeld Coll.) and Rovno (Representative Rovno Coll.) amber. Fossils incertae sedis are not counted; numbers of Empididae *s.l.* and Tipuloidea in the Sontag Coll. are considered unknown, because Sontag (2003) did not specify if she included Hybotidae, Microphoridae and Tipulidae under the above names, or separately. In Sontag Coll., Mycetophilidae are given under Mycetophilidae *s.l.*, otherwise Mycetophilidae *s.l.* are Mycetophilidae + Keroplatidae. Tipuloidea means Tipulidae + Limoniidae.

Family	Brighton Coll.	Sontag Coll.	Hoffeins. Baltic Coll.	Hoffeins Bitterfeld Coll.	Representative Rovno Coll.
Chironomidae	139 (42.2%)	1141 (42.2%)	1376 (37.5%)	2410 (33.9%)	137 (22.9%)
Sciaridae	52 (15.8%)	506 (18.7%)	728 (19.9%)	1562 (22.0%)	189 (31.6%)
Mycetophilidae <i>s.l.</i>	24 (7.3%)	230 (8.5%)	317 (8.6%)	795 (11.2%)	55 (9.2%)
Ceratopogonidae	20 (6.1%)	158 (5.9%)	224 (6.1%)	459 (6.5%)	29 (4.8%)
Cecidomyiidae	24 (7.3%)	114 (4.2%)	105 (2.9%)	202 (2.8%)	23 (3.8%)
Psychodidae	6 (1.8%)	89 (3.3%)	90 (2.5%)	109 (1.5%)	16 (2.7%)
Tipuloidea	5 (1.5%)	—	78 (2.1%)	123 (1.7%)	51 (8.5%)
Scatopsidae	—	3 (0.1%)	3 (0.1%)	14 (0.2%)	3 (0.5%)
Ptychopteridae?	1 (0.3%)	—	—	—	—
Simuliidae	1 (0.3%)	2 (0.1%)	1	6 (0.1%)	—
Mycetobiidae	—	1	3 (0.1%)	1	1 (0.2%)
Dixidae	—	—	1	2	—
Bibionidae	—	—	2	—	—
Nymphomyiidae	—	—	1	1	—
Corethrellidae	—	—	0	1	—
Dolichopodidae	38 (11.6%)	271 (10.0%)	486 (13.3%)	865 (12.2%)	64 (10.7%)
Phoridae	3 (0.9%)	65 (2.4%)	117 (3.2%)	328 (4.6%)	18 (3.0%)
Empididae <i>s.l.</i>	13 (4.0%)	—	110 (3.0%)	176 (2.5%)	7 (1.2%)
Rhagionidae	—	8 (0.3%)	12 (0.3%)	18 (0.3%)	4 (0.7%)
Syrphidae	2 (0.6%)	2 (0.1%)	3 (0.1%)	5 (0.1%)	—
Athericidae	—	—	—	2	—
Bombyliidae	—	—	1	0	1 (0.2%)
Opetiidae	—	—	1	0	—
Drosophilidae?	—	1	—	—	—
Xylomyidae	—	—	0	1	—
Acalyptata	—	—	8 (0.2%)	31 (0.4%)	—
Anthomyiidae?	1 (0.3%)	—	—	—	—
TOTAL	329	2702	3667	7111	598

Coll.) of insects *s.str.* Within the order (Table 4), the Representative Rovno Coll. contains half as many Chironomidae (22.9% vs., respectively, 42.2%, 42.2% and 37.5%); almost twice as many Sciaridae (32% vs. 16%; 19%, 20%); and 6.8 times as many Limoniidae (6.1% vs. 0.9% Brighton Coll. and 1.9% in Sontag Coll.). The proportion of Dolichopodidae is the same as in the Brighton Coll., that of Empididae *s.l.* is less (1.2% vs. 4.0%; 3.0% – in Hoffeins Baltic Coll.); while the proportion of Phoridae is more (3% vs. 0.9%; 2.4% in Sontag Coll.; 3.2% – in Hoffeins Baltic Coll.).

The Representative Rovno Coll. shows a deficiency of aquatic and subaquatic dipterans, particularly Chironomidae, while the number of families connected with leaf litter (“*Sciara* zone” according to Larsson 1978), such as Sciaridae, Limoniidae, Tipulidae, Psychodidae, Phoridae, Mycetophilidae and Keroplatidae is twice that in Brighton Coll. (55% vs. 27%) (Table 4). This conclusion is further supported by the fact that in the Rovno amber, there are many forms connected with leaf litter, even among the Chironomidae.

The Rovno amber fauna also shows a deficiency of hygro- and hydrophilous Coleoptera. Baltic amber collections contain 14–23% Helodidae (Klebs 1910; Hieke &

Pietrzeniuk 1984), while in the Total Kiev Coll., they account for only 7% out of 200 beetles. On the contrary, leaf-litter forms of the “*Sciara* zone”, particularly Staphylinidae, Scydmaenidae, Leiodidae (Leiodidae from the Rovno amber can also be referred to the “*Sciara* zone”) and Ptiliidae are abundant. Staphylinoids are extremely numerous and account for 23% of all beetles. Ptiliids account for 4.6% of all Representative Rovno Coll. beetles (not 3.5%, as was erroneously mentioned by Polilov & Perkovsky 2004). They are represented by two specimens of *Ptilium* (found in one piece of amber) and by the holotype of *Ptinella rovnoensis* Polilov & Perkovsky.

Among hymenopterans, the proportion of ants is almost the same in both collections – 43% vs. 44% (49.8% in Sontag Coll.). In the Total Kiev Coll. (3600 inclusions, 2735 insects), ants account for 6% of all insects (not 7.6% as given by Dlussky & Rasnitsyn 2003) (5.8% in Sontag Coll.). Worth mentioning is the higher abundance of myrmicine and lower abundance of *Ctenobethylus goepperti* (Mayr) in the Representative Rovno Coll. (*C. goepperti* represents 29.7% of all ants vs. 59.1% in the Brighton Coll.; Table 3). There are no pieces of amber containing more than one specimen of *C. goepperti* in the Representative Rovno Coll., while in the Brighton Coll. 46.2% of *C. goepperti* are found in such syninclusions. In addition, other hymenopterans show obvious differences: there are three times as many Scelionidae in the Representative Rovno Coll. (18.4 vs. 6%), while Diapriidae are less numerous (9.2% vs. 12%) (Table 2). Other families of hymenopterans are too few in number to justify comparison (the larger number of ichneumonids, compared with braconids in the Brighton Coll., is undoubtedly a sample bias). The same holds true for the other arthropod groups, which are represented in the examined collection, but are not included in the comparisons.

CONCLUSIONS

A comparison of the representative samples of the Baltic and Rovno amber points toward independent origins of their respective faunas. The differences observed are in part indicative of their ecological nature. For instance, compared to the Baltic assemblage, the Rovno amber is distinctly impoverished in aquatic and coastal arthropods while enriched with the leaf-litter dwellers of the “*Sciara* zone”. Rarity of aphids in the Rovno amber suggests a warmer, possibly subtropical climate of the Ukraine Crystalline Rock Massif in the Late Eocene, while a higher number of Scelionidae in the Rovno assemblage is indicative of a more xeric environment. This is in contrast to the Baltic amber, where Diapriidae are more abundant.

The age of the Baltic amber and stratigraphic correlation of the amber-bearing Prussian Formation are considered in some detail. It is concluded that proposal of a Middle Eocene (Ypresian–Lutetian) age contradicts a wide array of the palaeontological, radiological, and stratigraphic data and thus cannot be accepted on the basis of available evidence.

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